

# The fossil alga *Girvanella* Nicholson & Etheridge



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## Synopsis

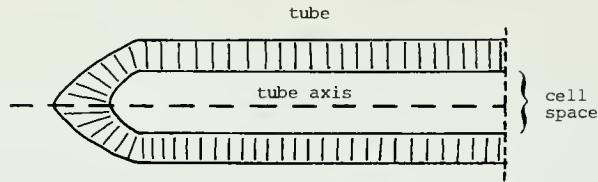
This group of microfossils is reviewed and compared with its modern counterpart, the Cyanophyta. *Girvanella* consists of carbonate tubes, believed to have formed in and around the sheaths of filamentous blue-green algae. The characteristics of the genus are discussed in terms of those of the living forms, and an emended generic diagnosis is offered to take account of modern knowledge. The ultrastructure of the fossil consists of equidimensional and prismatic grains in the micrite to fine spar range, with the prisms arranged perpendicularly to the tube axis. This is similar to *Rothpletzella* Wood, from preliminary studies. Specific subdivision of *Girvanella* is considered briefly, and a list of the species is provided with full references. Suggestions for an approach to revision of the specific systematics are made, with emphasis on sampling along single horizons to allow clinal variation to be studied.

## Introduction

The genus *Girvanella* was defined by Nicholson & Etheridge (1878 : 23) as containing certain calcareous tubular fossils. It was first described from the Stinchar Limestone of south Scotland, which is of Caradocian (Middle Ordovician) age. The biological source of the fossil was the subject of some debate during the latter part of the nineteenth century (*cf.* Green 1959 : 41). It was first described as a foraminifer, but was then transferred to the Cyanophyta *sensu* Smith 1938. Attempts have been made to move it to the Chlorophyta *sensu* Smith 1938, for example by J. H. Johnson (1961 : 194), and recently some related forms have been described as members of the Rhodophyta *sensu* Smith 1938 by Korde (1973 : 212).

The Porostromata of Pia (1927 : 37), the group to which most workers believe *Girvanella* belongs, is itself poorly understood. Pia's definition is brief, and no general study of the organisms contained in it has been published. The group was erected to hold fossils of tubular construction, which resemble modern calcified filamentous cyanophytes. Unfortunately, little is known about these plants either, except that they do not seem to occur in the marine environments to which most *Girvanella* species are confined.

(a) Longitudinal section.



(b) Cross and oblique sections.

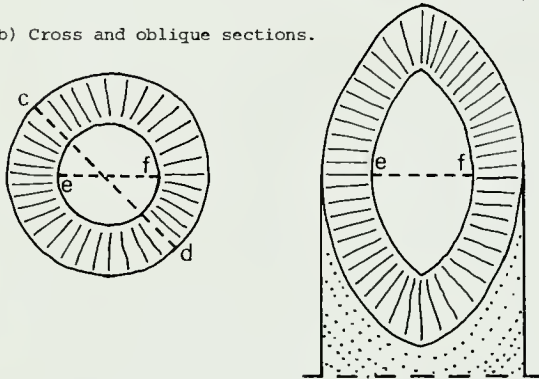


Fig. 1 Generalized diagrams of *Girvanella*, with terminology. ef—true internal diameter. cd—external diameter.

Girvanellids appear to be simple fossils, with few features suitable for use in systematic subdivision. This has led to the introduction of a great number of species, with overlapping and subjectively-defined characteristics. The classification has become unwieldy and confusing, and does not seem in any real way to reflect the biology of the original organisms.

The intention of this paper is to review the generic concept *Girvanella*, to present an analysis of a sample of the fossil taken from the Stinchar Limestone, and to attempt a more representative generic diagnosis and description. The relationship of the genus to modern cyanophytes will be considered, and its specific subdivision discussed. Morphological terms used are as follows. Filament: the tube and cell space. Growth: a group of filaments which seem to have formed an original nodule, cluster or sheet. Density: percentage volume of filaments in a growth. Others are illustrated in Fig. 1.

The systematic criteria of Pia (1927) are used for the higher taxa of fossil algae, and Tilden (1910) has been used as a source for the Recent taxa.

The term 'carbonate tube' is employed for the fossil structures themselves. It has no biological implications, and is therefore preferable to the often-used 'wall' or 'sheath'. The former could be confused with 'cell wall', which has little relation to the carbonate tube, while a cyanophyte sheath is a mucilaginous, extracellular part of the cell envelope and is rarely preserved.

### Sources of material and methods of study

The Stinchar Limestone rests unconformably on the Ballantrae ophiolite sequence, with a zone of serpentinite débris at the contact (Table 1). Most of the Limestone formation is exposed at Aldons Quarry (nat. grid ref. NX 197896), south of Girvan, Ayrshire (*cf.* Williams 1962). *Girvanella* was first described from samples collected at another quarry about 6 km NE of Aldons, Tormitchell (NX 235944) (Nicholson & Etheridge 1978). Aldons Quarry was preferred to Tormitchell because the limestone sequence is relatively undisturbed, and because it is not at present (1980) being quarried.

Samples were collected at intervals of a maximum of 0.30 m or less from the top of the ophiolites, through the entire limestone sequence. A total of 34 thin sections were cut from these samples, as shown on Table 1, and all were studied for mineralogy and general palaeontology. Five samples were selected for detailed study of *Girvanella* with a binocular

**Table 1** The Stinchar Limestone at Aldons Quarry.

Field characteristics	level (cm) of base	level (cm) of thin sections	% <i>Girvanella</i>
Benan Conglomerate (above thrust)	variable	—	—
0 to 10 cm mylonite		—	—
micrite with crystal elongation lineation, some spar lenses	2000	—	—
no nodules, some neomorphic spar		—	—
nodular zone at base	1620	1658	low
fewer nodules	1510	—	—
friable micrite with many nodules	960	—	—
slumped, with poor and very undulose bedding; nodular with micritic matrix.	490	931 833* 750	— low high
grey micrite with poor bedding	450	461, 470*	high
banding of fine and coarse layers, laminated, fine serpentinite debris in micrite	300	439, 434, 417 400, 388 338	low low
conglomeratic, serpentinite pebbles in micritic matrix; 1 m-thick bedding.	155	230, 221, 195* 180*, 165*, 155*	appears
(1 m gap)	57	—	
soft green silts	0	(5 thin sections)	none
Ballantrae Ophiolites			

\*section used in population study.

Table 2. A list of the species of *Girvanella*.

Species	Key to Fig. 7	Original generic assignment	Author	Approximate age
<i>involutans</i>		( <i>Nicholsonia</i> )	Korde 1973	Upper Proterozoic
<i>antiqua</i>	1		Dawson 1896	Lower Cambrian
<i>bayanolkolica</i>		( <i>Batinevia</i> )	Maslov 1937	Lower Cambrian
<i>composita</i>		( <i>Nicholsonia</i> )	Korde 1973	Lower Cambrian
<i>deceptans</i>		( <i>Fistulella</i> )	Korde 1973	Lower Cambrian
<i>glomerata</i>		( <i>Nicholsonia</i> )	Korde 1973	Lower Cambrian
<i>grandis</i>		( <i>Nicholsonia</i> )	Korde 1973	Lower Cambrian
<i>lineata</i>		( <i>Botominella</i> )	Reitlinger 1959	Lower Cambrian
<i>manchurica</i>	2		Yabe & Osaki 1930	Lower Cambrian
<i>ornata</i>		( <i>Kenella</i> )	Korde 1973	Lower Cambrian
<i>ramosa</i>		( <i>Batinevia</i> )	Korde 1966	Lower Cambrian
<i>sanashiykgorica</i>	3	( <i>Fistulella</i> )	Korde 1973	Lower Cambrian
<i>sibirica</i>	4		Maslov 1956	Lower Cambrian
<i>mexicana</i>	50	( <i>Siphonema</i> )	J. H. Johnson 1952	Lower Cambrian
<i>incrustans</i>		(range extends from Cambrian to Silurian, and Jurassic).	Bornemann 1886	Cambrian
-----				
<i>grandis</i>	5		Banks & Johnson 1957	Llanvirn to Llandeilo
<i>atratius</i>		( <i>Strophochetus</i> )	Seely 1902	Llanvirn to Llandeilo
<i>brainardi</i>		( <i>Strophochetus</i> )	Seely 1902	Llanvirn to Llandeilo
<i>prunus</i>		( <i>Strophochetus</i> )	Seely 1902	Llanvirn to Llandeilo
<i>ocellatus</i>		( <i>Strophochetus</i> )	Seely 1885	Llanvirn to Llandeilo
<i>richmondense</i>		( <i>Stromatocerium</i> )	Miller 1882	Llanvirn to Llandeilo
<i>tasmaniensis</i>	6		Banks & Johnson 1957	Llanvirn to Llandeilo
<i>ambigua</i>	7		Luchina, <i>in</i> Nikitin <i>et al.</i> 1974	Middle Ordovician
<i>convoluta</i>	8		Luchina, <i>in</i> Nikitin <i>et al.</i> 1974	Middle Ordovician
<i>problematica</i>	9		Nicholson & Etheridge 1878	Caradocian
<i>problematica lumbricalis</i>	10		(Nich. & Eth.) Wood 1957	Caradocian
<i>problematica montiformis</i>	11		Hoeg 1932	Caradocian
<i>(problematica spiralis)</i>	12		Hoeg 1932	Caradocian
	13: this form has been rejected		Lewis 1942	Caradocian

<i>problematica typica</i>	14					
<i>incrustans</i>	50	( <i>Sphaerocodium</i> )	Hoeg 1932 Bornemann 1886		Caradocian Ordovician	
<hr/>						
<i>siluriana</i>	15	( <i>Sphaerocodium</i> )	Parks 1933 (Roth.) Dricot & Tsien 1977 Chapman 1907		Up. Llandoveryan to Wenlockian Wenlockian	
<i>bornemannii</i>	16		H. M. Johnson 1966		Wenlockian	
<i>conferta</i>	17		H. M. Johnson 1966		Wenlockian	
<i>eflusa</i>	18		H. M. Johnson 1966		Wenlockian	
<i>fragila</i>	19		H. M. Johnson 1966		Wenlockian	
<i>media</i>	20		H. M. Johnson 1966		Wenlockian	
<i>prolixa</i>	21		H. M. Johnson 1966		Wenlockian	
<i>pusilla</i>	22		H. M. Johnson 1966		Wenlockian	
<i>ramosa</i>	23		H. M. Johnson 1966		Wenlockian	
<i>sarmentata</i>	24		Chapman 1907		Wenlockian	
<i>wetheredii</i>	25		H. M. Johnson 1966		Wenlockian to Lower Ludlovian	
<i>incompta</i>	25					
<i>incrustans</i>	50	( <i>Siphonema</i> )	Bornemann 1886		Silurian	
<hr/>						
<i>maslovi</i>	26		Shušskii 1973 Bilan & Golonka 1973		Lower Devonian Famenian	
<i>ducii chtvashovi</i>	27		Pia 1932 (range extends from Devonian to Permian)		Upper Devonian Upper Devonian	
<i>amplefurcata</i>	27	( <i>Sphaerocodium</i> )	(Roth.) Dricot & Tsien 1977			
<i>zimmermanni</i>	28		(Pia) Wood 1963 Pia 1937		Lower Tournaisian Tournaisian	
<i>ottonosia</i>	29		Garwood 1931 (Garwood) Wood 1963		Upper Tournaisian Upper Tournaisian	
<i>stamenia</i>	30		(Weth.) Wood 1941		Tournaisian to Lower Viséan	
<i>nicholsoni</i>	31		Conil & Lys 1964		Lower to Middle Viséan	
<i>densa</i>	32		Conil & Lys 1964		Lower to Middle Viséan	
<i>distans</i>	33		Wethered 1890		Upper Viséan	
<i>ducii</i>	34		(Weth.) Wood 1963		Upper Viséan	
<i>ducii</i>	35		Wethered 1890 (Chapman) Wood 1963		Upper Viséan Upper Viséan	
<i>incrustans</i>	34		Maslov 1949		Lower Carboniferous	
<i>wetheredii</i>	35		Paul 1937		Lower Carboniferous	
<i>ducii kasakiensis</i>						
<i>liebustii</i>						

Species	Key to Fig. 7	Original generic assignment	Author	Approximate age
<i>silesiaca</i>	36		Paul 1937	Lower Carboniferous
<i>maplewoodensis</i>	37		J. H. Johnson 1946a	Namurian to Westphalian
<i>moorei</i>	38		J. H. Johnson 1946b	Westphalian
<i>magna</i>	39		J. H. Johnson 1946b	Upper Westphalian
<i>ducii chuvashovi</i>	26		Bilan & Golonka 1973	Upper Carboniferous
<i>sinensis</i>	40		Yabe 1912	Upper Carboniferous
<i>johnsoni</i>	41		Kulik 1973	Carboniferous
-----				
<i>ducii chuvashovi</i>	26		Bilan & Golonka 1973	Lower Permian
<i>grabau</i>	42		Paul 1938	Lower Permian
<i>subparallela</i>			Flügel & Flügel-Kahler 1980	Lower Permian
<i>catenoides</i>	43		Homan 1972	Lower to Middle Permian
<i>pernica</i>	44		Pia 1937	Middle Permian
<i>texana</i>	45		J. H. Johnson 1950	Permian
-----				
<i>incrustans lucii</i>	46		Wethered 1890	Bathonian
<i>pisolitic</i>	47		Wethered 1889	Bathonian
<i>minuta</i>	48		Wethered 1890	Bathonian
<i>intermedia</i>	49		Wethered 1890	Bathonian
<i>incrustans</i>	50	( <i>Siphonema</i> )	Bornemann 1886	Jurassic
<i>jurassica</i>		( <i>Symphloca jurassica</i> )	Dragastian 1975	Jurassic
		Frém. & Dan.; <i>G. minuta</i> Weth.)		
<i>tosaensis</i>	51		Yabe & Toyama 1928	Lower Mesozoic
-----				
<i>minima</i>	52		Romanes 1916	Albian
<i>palustris</i>	53		Colin & Vachard 1977	Middle Cretaceous

Güvenç (1965) describes the following species as part of a Ph.D. thesis: *G. magna goksienensis*, Upper Visean. *G. magna yatani*, Upper Carboniferous. *G. kordei*, Upper Carboniferous to Lower Permian. *G. embergeri*, Lower Permian. Gollestaneh has found several species dating from the Cambrian, in Iranian deposits (personal communication), but the descriptions are not published as yet. *G. shirazica* (Liassic to Oxfordian) is mentioned by Gollestaneh (1974), but it has not been possible to obtain a diagnosis of the species.

microscope. Acetate peels were also tried, but were found unsuitable because of the fine grain-size of the limestone, and because of certain artefacts inherent in their use. Registered numbers given with the half-tone illustrations (Figs 2, 3, 5) are those of the British Museum (Natural History), Dept. of Palaeontology.

Measurements were made with an eyepiece graticule. This method gives results to about the same degree of accuracy as Wood's (1957: 24) technique of measuring from photographic prints. The correction of errors introduced by photographic processes is cancelled by the small scale of the graticule.

The number of tubes present in growths varied a great deal, as did the degree of preservation. Frequently the boundaries of a tube were obscured by neomorphism or by contact with other tubes. It was necessary to measure both diameters for each tube since comparisons of the two diameters were needed. For this reason, only tubes with both inner and outer boundaries clearly apparent were measured, and other tubes were ignored. All the tubes, up to a total of ten, with both boundaries present were measured in each growth. As a result some growths are represented by measurements on only one or two tubes, but no justification could be found for omitting them. In any case measurements were analysed by considering the entire sample, rather than individual growths. Ten was chosen as the upper limit because most growths had only ten or fewer suitable tubes. Where two distinct size-ranges occurred in the same growth, ten tubes were measured from each.

A plane section cut through tubes arranged more or less randomly will contain a range of sections of tubes from cross to longitudinal. Perfect cross sections are circular, because of the cylindrical shape of the tubes, but oblique sections are elliptical (Fig. 1). It can be shown that the smallest diameter of such an oblique section is a true diameter of the tube. All measurements have therefore been made on this smallest diameter. The tube thickness may have irregularities, so that estimation was sometimes necessary for measurements of the external diameter. However, it was possible in most cases to measure the two diameters along the same line.

For scanning electron microscopy, rock samples were prepared by smoothing rock slices on carborundum powders and polishing with a series of diamond laps, finishing with a 1  $\mu\text{m}$  lap. This was followed by etching for 30 secs in 1 vol. % HCl. The slices were then attached to specimen stubs with a conducting paint, Durofix or double-sided sellotape, and were coated with gold-palladium in a vacuum-evaporator.

Samples of Recent algae were obtained from a variety of sources, either by personal collection or through the courtesy of other workers. These samples were stored at 3° C, in 0.8% glutaraldehyde buffered to pH 7.4, and were prepared for electron microscopy as follows:

1. Immersion fixation in 2.5% glutaraldehyde, buffered to pH 7.4 with  $\text{KH}_2\text{PO}_4$  and  $\text{K}_2\text{HPO}_4$ , for two hours.
2. Washing in several changes of buffer.
3. Immersion in 1%  $\text{OsO}_4$ , in buffer, for 30 minutes.
4. Gradual transfer to water-free acetone.
5. Critical point drying.

The scanning electron microscopes (S.E.M.) used were Cambridge S2A models, operated at 18 KV at lower magnifications and at 28 KV to 30 KV at magnifications of 5000 $\times$  or more. The final aperture diameters were 200  $\mu\text{m}$  for lower and 140  $\mu\text{m}$  for higher magnifications. Stubs were held at 30° to the electron beam to reduce the effects of charging, with a working distance of about 10 mm.

### Historical review

Species of *Girvanella* have been described, under various generic names, from rocks of Upper Proterozoic (Korde 1973: 212) to Middle Cretaceous (Colin & Vachard 1977) age. A list of species is given in Table 2.

*Girvanella* was first described by Nicholson & Etheridge (1878 : 23) as an agglutinating foraminiferan related to *Rhizammina algaeformis* Brady. They gave the specific name *problematica* to their fossil, for convenience, and provided the following diagnosis:

*Generic characteristics*: 'Microscopic tubuli, with arenaceous or calcareous (?) walls, flexuous or contorted, circular in section, forming loosely compacted masses. The tubes apparently simple cylinders, without perforations in their sides, and destitute of internal partitions or other structures of a similar kind'.

*Specific characteristics*: 'Tubes from 1-600th to 1-700th of an inch in diameter, not observed to taper, twisted together in loosely reticulate or vermiculate aggregations of a rounded or irregular shape, which seem to be mostly from 1-20th to 1-10th of an inch across'.

Nicholson (1888 : 22) gave a further description of the organism, but did not redefine it. Apart from assigning a different range of diameters to the genotype (16  $\mu\text{m}$  to 40  $\mu\text{m}$ ) he added nothing to the original publication, and still believed the organism to have been a foraminiferan. This view was held by some workers for a long time, Rhumbler (1895) proposing a subfamily Girvanellinae of the Rhabdamminidae Rhumbler to contain the genus.

Seely (1885) described a genus of calcareous sponge, *Strephochetus*, from Middle Ordovician limestones in Vermont, and in 1886 Bornemann described *Siphonema* from Sardinian deposits of the same age. Bornemann compared his material with epilithic cyanophytes, and considered that *Siphonema* was related to them. Hinde (1887 : 227) recognized *Strephochetus* and *Siphonema* to be synonyms of *Girvanella*, but disagreed with both suggested affinities.

Rothpletz (1891 : 301) assigned *Girvanella* to the Codiaceae ((Trevis) Zanardini 1843) because of the dichotomous branching shown by some species, and its similarity to *Sphaerocodium* Rothpletz 1891. The latter has been assigned to the Siphonae, a taxon containing both the Codiaceae and Dasycladaceae (Endlicher) Cramer 1888. This assignment to the green algae was accepted by Brown (1894 : 203).

Wethered (1893 : 246) accepted that some forms of *Girvanella* appeared to have been plants, and might have been calcareous algae. In the discussion of this paper (p. 248), Reid suggested that the calcareous tubes typical of *Girvanella* were the result of inorganic encrustations on filamentous plants. Seward (1898 : 125) and Pollock (1918 : 255) compared *Girvanella* to the calcified sheaths of some Recent Cyanophyta, thus confirming Bornemann's (1886) opinion.

Pia (1927 : 37) placed *Girvanella* and similar genera in an artificial group, the Porostromata. This was accepted for some years. In 1935 Frémy & Dangeard proposed that the Jurassic species *G. minuta* Wethered should be renamed *Symploca jurassica*, because of its resemblance to the Recent species *S. hydnoides* Kutz. However, Johnson & Høeg (1961 : 54) expressed doubts about the assignment of *Girvanella* to the Cyanophyta, and suggested that it was a member of the Chlorophycophyta. This proposal seems to have been based on his own removal of many of the Porostromata to the Codiaceae, and also on the belief that Frémy & Dangeard had described *G. minuta* as a chlorophyte. Riding (1975 : 174) has restored these genera to the Porostromata. Dricot & Tsien (1977), in a discussion of the validity of the genus *Rothpletzella* Wood 1948, have pointed out the partial synonymy between *Girvanella* and *Sphaerocodium* Rothpletz 1891. Several of the species of the latter were therefore assigned to *Girvanella* by these authors, in part or completely (Table 2, p. 83).

Korde (1973 : 212) has mentioned several Upper Proterozoic and Lower Cambrian genera which appear to be girvanellids. The genera involved are *Nicholsonia* Korde, *Fistulella* Korde, *Botominella* Reitlinger (1959), *Kenella* Korde, and *Batinevia* Korde (1966). Mamet & Roux (1975) have commented on the resemblance between the last three and *Girvanella*. Korde (1973) proposes a new class of Rhodophyta, the Protobangiophyceae Korde, to contain these genera. But some of the descriptions of the protobangiophycean genera seem to bear little resemblance to the figures provided, and the reasons for the separation of these forms are not expressed in such a way that they can be evaluated.



*Nicholsonia* in particular seems to have been interpreted on the understanding that the original organism was a member of the Rhodophyta. Structures which are absent from the fossil are said to have been uncalcified. Korde's descriptions are not included in the systematic analysis below, as it is difficult to reconcile her accounts with other descriptions.

Riding (1977) has related the impregnated sheath of *Plectonema gloeophilum* Borzi, a modern species with rare branching, to *Girvanella*, and extends the range of the fossil to Recent times on this basis. However, the branching habit of *Plectonema* does not agree with the 'simple cylinders' definition of *Girvanella* (Nicholson & Etheridge 1878: 23). The ultra-structures of the carbonate are also rather different, that of *P. gloeophilum* consisting of calcite needles in various orientations. *Girvanella* tubes comprise equidimensional micrite and radially-arranged needles, the structure having greater regularity and much lower porosity (Fig. 2).

### The genus *Girvanella*

Further descriptive remarks can now be added to the original definition of the genus (Nicholson & Etheridge 1878). Growths vary in size from single tubes to clusters more than a centimetre across. Growths with many tubes may be almost circular in section, completely irregular, or in some intermediate form, and may have a core body such as a detrital particle or, more commonly, another fossil. The boundaries between growth and rock matrix may be distinct, eroded, micritized, diffuse or neomorphosed. Often the matrix seems to have neomorphosed more easily than the carbonate tubes. Fig. 3 shows a range of growth habits from the Stinchar Limestone. In addition to the problems of defining the genus *Girvanella* some confusion has arisen in its subdivision. A list of species is given in Table 2, pp. 82-84, in which there are about 40 Lower Palaeozoic taxa. Only a few of these have diagnoses not contradicting the generic diagnosis, as shown in Table 3, and many have indistinguishable characteristics.

The holotype of *G. problematica* Nicholson & Etheridge, the type species of the genus, has been destroyed. Wood (1957: 23) discovered this and designated a neotype for the species. However, although he did not emend the generic diagnosis of Nicholson & Etheridge (1878), he redescribed the type species in a way which differs from the original generic diagnosis. This anomaly means that *Girvanella* and its type species *problematica* are still defined according to Nicholson & Etheridge (1878). Wood's neotype is kept in the British Museum

Table 3 Lower Palaeozoic species ascribed to *Girvanella* with characteristics contradicting the original generic definition; brackets indicate observations made from figures.

Simple cylinders	Branching	( <i>atratus</i> ) ( <i>brainierdi</i> ) <i>effusa</i> <i>fragila</i> <i>grandis</i>	<i>incompta</i> <i>media</i> <i>mexicana</i> <i>moniliformis</i> <i>ocellatus</i>	<i>problematica</i> * <i>p. lumbricalis</i> <i>p. typica</i> <i>prolixa</i> ( <i>prunus</i> )	<i>pusilla</i> <i>ramosa</i> <i>sarmenta</i> <i>sibirica</i> <i>tasmaniensis</i>
	Constrictions	<i>conferta</i>	<i>effusa</i>	<i>problematica</i>	<i>ramosa</i>
Loose packing	High density	<i>conferta</i> <i>convoluta</i> ( <i>effusa</i> ) <i>incompta</i>	( <i>manchurica</i> ) <i>media</i> <i>ocellatus</i> <i>problematica</i> *	<i>prolixa</i> <i>pusilla</i> ( <i>ramosa</i> ) <i>sarmenta</i>	( <i>siluriana</i> )
	Adherence	<i>effusa</i> <i>fragila</i>	<i>incompta</i> <i>media</i>	<i>prolixa</i> <i>pusilla</i>	<i>ramosa</i> <i>sarmenta</i>
Septation		<i>conferta</i>	<i>problematica</i> *	<i>prolixa</i>	

\*as emended by Wood (1957).

(Natural History) collection, registration number V 34566, and since it does in fact conform to the original generic diagnosis, it is accepted here as the neotype of *Girvanella*.

Considerable information has accumulated since 1878 about both *Girvanella* itself and the Cyanophyta. Nicholson & Etheridge's (1878) diagnosis needs to be re-examined and related to this new body of information. To facilitate this, the characteristics used to define the genus will be considered: (1) microscopic; (2) tubular; (3) arenaceous or calcareous; (4) sinuous; (5) circular in cross section; (6) low growth density; (7) simple cylinders; (8) imperforate; (9) no septa or other internal structures.

Of these, points 1, 2, and 8 have never been disputed. Most species have been described as circular (point 5), but J. H. Johnson (1950 : 61) gave *G. texana* as 'nearly circular'. Wood (1963 : 26) described irregular tubes, attributing them to *post mortem* collapse. No non-calcareous tubes have been reported (3), although some associations with iron oxide or pyrite have been published (H. M. Johnson 1966 : 51; Lewis 1942 : 52). Playford *et al.* (1976 : 558) noted that bacteria are more likely to be responsible for such relationships than the algae themselves. Silicified *Girvanella* has also been described (Lewis 1942 : 51), but this example was a secondary replacement.

The hollow nature of the tubes (2) has never been questioned, and Lewis (1942 : 52) gives evidence for it. However, both branching and constrictions (7) have been described by several authors (Table 3). The figures provided in these cases commonly show tubes which cross or bend out of the plane of section, leading to misinterpretation (*cf.* H. M. Johnson 1966 : pl. 12). Septate girvanellids (9) have also been described, but these reports are the result of observation of refraction across grain boundaries within the cell space (Wood 1957 : pl. 5). Fig. 2, opposite, illustrates the causes of apparent branching, constrictions and septa.

Many authors have described growths with close-packed, adherent tubes, although Nicholson & Etheridge (1878) describe the genus as being loosely-compacted. In fact a great variety of growth densities (defined here as the ratio of tube volume to matrix volume in a growth) occurs in many populations, and the value of density as a generic or specific characteristic needs reconsideration in the light of population studies. The same applies to tube sinuosity (4). Some examples demonstrating the variability of single populations are given in Fig. 3.

### *Girvanella* and Recent cyanophytes

Some modern Cyanophyta will calcify under natural conditions, when an excess of calcium is present, although they will not do so readily in culture. Lewin (1962) and Golubić (1973) have given reviews of the subject, and Pentecost (1978) has conducted a detailed study of cyanophyte calcification.

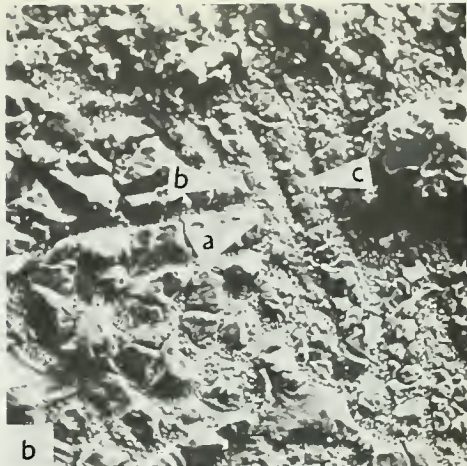
It is usually said that cyanophytes calcify only in freshwater environments, although many fossils, supposedly calcified cyanophytes, are primarily marine in origin. Monty (1977) has discussed the matter in terms of stromatolites. Some Recent forms do calcify in regions where storms may cover them with sea water from time to time, and further research may find fully marine forms which calcify.

Almost the only thing which seems to be common to the environments in which cyanophytes calcify is the high calcium level. Some calcium is clearly necessary, but

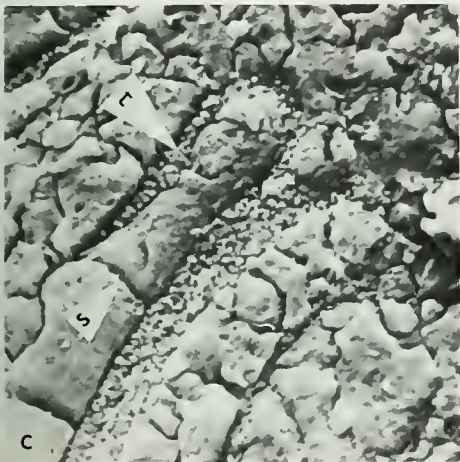
**Fig. 2** Fine structure of *Girvanella* and *Rothpletzella*. (a), *Girvanella* with apparent branching. White lines mark tube directions. Bar = 7  $\mu\text{m}$ . (V 60469). (b), *Girvanella* with apparent branching due to crossed tubes (SEM). Note the rounded ends of tubes a and b, against c. Bar = 10  $\mu\text{m}$ . (V 60473). (c), apparent septa, marked s. The tube itself (t) comprises equidimensional micrite, but this is missing from the 'septae'. They are grain boundaries, lying across the tube axis. Bar = 5  $\mu\text{m}$ . (V 60473). (d), tubes with a prismatic ultrastructure (p). Bar = 10  $\mu\text{m}$ . (V 60473). (e), *Rothpletzella* with equidimensional micrite forming its tubes (t). Bar = 5  $\mu\text{m}$ . (V 60103a). (f), *Rothpletzella* with radial prisms (p). Bar = 10  $\mu\text{m}$ . (V 60103a).



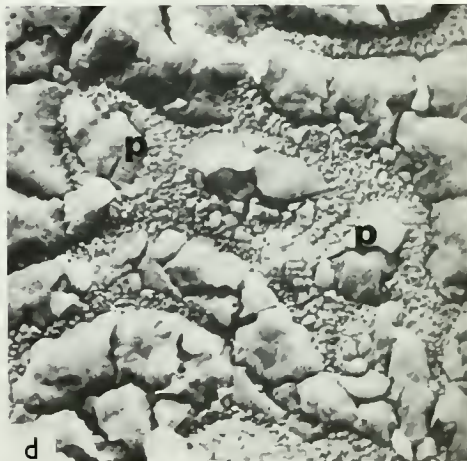
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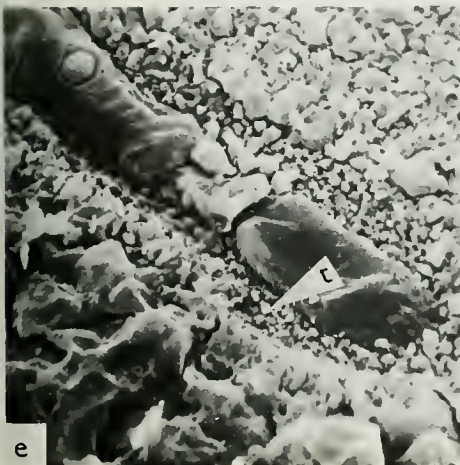
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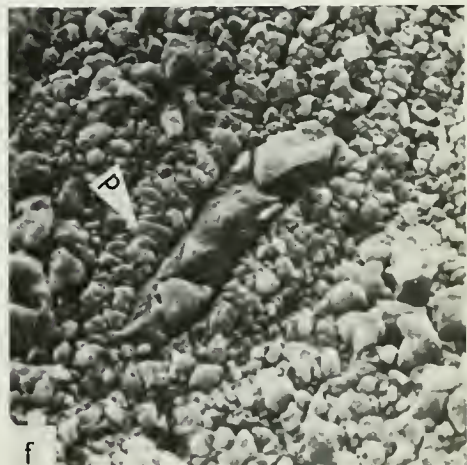
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blue-green algal deposits seem to occur only in waters which are saturated with it. Neither high light intensities nor warmth are essential, and water-flow rates vary considerably. These generalities apply to the group as a whole, however, and individual strains may be more exacting. This may be the cause of many of the difficulties met in laboratory studies of calcification.

It seems then, that the ecology of modern cyanophytes is of little help in the interpretation of fossil forms. That *Girvanella* had a wide ecological range implies only that several biologically distinct taxa were involved. The genus occurs in shallow-water marine limestones (from faunal evidence), and may be quite rare or may form 80% of the rock volume (Williams 1962 : 19). It is found with benthic faunas in calcareous muds or silts, and in reef environments. Often it is the only cyanophyte represented, but other porostromates may be present and calcified eucaryotes may also occur. Palaeoecological evidence suggests growth in quiet or only moderately turbulent conditions, but such estimates are questionable. It is likely that uncalcified algal mats were present in the same environments, stabilizing sediments and preventing the development of current structures.

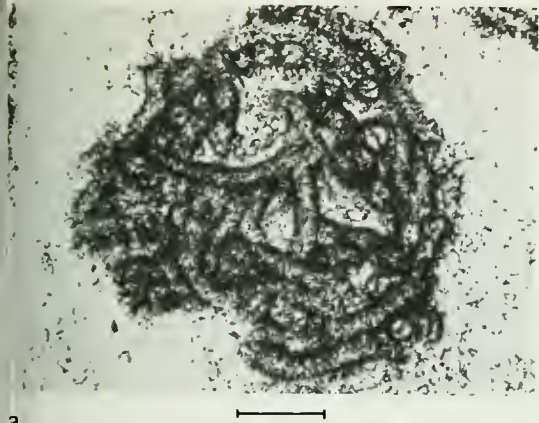
Modern cyanophytes may either impregnate or encrust their mucilaginous sheaths. Many organisms do both. The nature of the internal diameter of the carbonate tube depends on these differences. Distinguishing between them is therefore important: this matter is considered in more detail below. The carbonate itself is normally calcitic and low in magnesium, iron and strontium, although Monty & Hardie (1976 : 463) have described carbonates with 16 mole % Mg, formed in association with *Scytonema myochrous* (Dillwyn) Agardh. Modern cyanophyte carbonates are therefore stable in most cases, and are not subject to rapid diagenesis. However, since most modern calcifying blue-greens are freshwater organisms, comparisons with the predominantly marine *Girvanella* should be drawn with caution.

The fine structures of modern cyanophyte carbonates vary considerably, from the acicular type described by Gleason (1972 : 155) to the micritic textures figured by Schäfer & Stapf (1978 : fig. 4). Flajs (1977) describes the carbonates of three members of the Rivulariaceae as similar to those of *Chaetophora* (Chlorophyta). In these the filaments become encrusted with very fine calcite grains, which merge to form larger aggregates. Flajs believed all calcifying cyanophytes to follow this pattern. The close similarity between them and certain green algal carbonates, which he demonstrated, is of considerable interest.

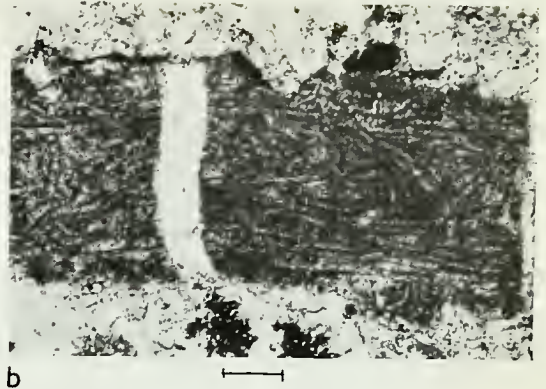
Differences certainly occur from cyanophyte to cyanophyte, as shown in Fig. 4, but the differences lie in grain size and arrangement, rather than in grain shapes. Acicular carbonates like those described by Gleason (1972) or Krumbin & Potts (1978) are comparatively rare. There is no clear evidence that these ultrastructures can be used to distinguish cyanophyte genera in the biological sense, but some similarities within families seem to exist, especially if taken with other factors (Danielli in prep.). A description of the ultrastructure of *Girvanella* has, then, a place in the diagnosis of the genus. Some similarities are shown by the fine structures of *Girvanella* and *Rothpletzella* (Fig. 2, p. 89), emphasizing the close relationship of these two genera.

Early systematic studies of modern Cyanophyta were based on morphological and ecological grounds (see Geitler 1932). Drouet (1962, 1963) showed that cyanophyte morphology is very dependent on the environment of growth, and considerably condensed the number of taxa in his revised classification of the Oscillatoriaceae (Drouet 1968). The systematic study of Rippka *et al.* (1979) seems to be even more revolutionary, but will put

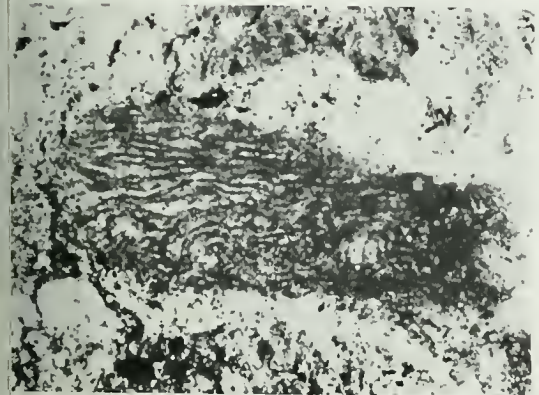
Fig. 3 Growth habits of *Girvanella* in the Stinchar Limestone at Aldons Quarry. (a), moderate density, variable parallelism and adherence. Bar = 20  $\mu$ m. (V 15956). (b), elongate growth with external zone of subparallel adherent tubes, and internal zone of random adherent tubes, high density throughout. Bar = 100  $\mu$ m. (V 60470). (c), subparallel tubes with lower density and adherence. Bar = 50  $\mu$ m. (V 60471). (d), high density adherent tubes with random arrangement. Two tubes are in complete circles (c). Bar = 20  $\mu$ m. (V 15965). (e), isolated tube with a cement overgrowth. Bar = 5  $\mu$ m. (V 60472).



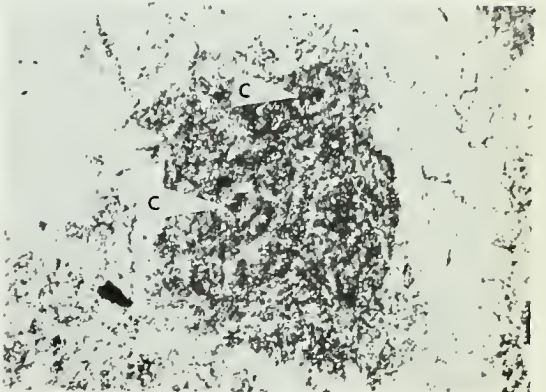
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identification on a more objective basis. The organisms are cultured on standard media, so that a comparison of genotypes becomes possible. The method has been discussed by Whitton, Holmes & Sinclair (1978 : 64) and by Potts & Whitton (1980).

Elliott (1964 : 569) has described possible heterocysts in the Triassic form *Zonotrichites lissaviensis* Bornemann (1887). However, heterocysts and akinetes are not normally distinguishable in fossil material. H. M. Johnson's (1966 : pl. 6) example of the former in *Girvanella* may be neomorphic spar. In fossil algae, gross filament morphology is the principal tool available to the systematist. Thus whether or not a particular characteristic is useful should be decided on the basis of its biological nature. If a size or shape variation can be shown to have some direct relationship to the genotype of the organism, it may be of great value. Indeed, it is on this that identification by standard culture is based. If all the organisms tested give the same response under the same conditions, the assumption that they have the same genotype may be justified.

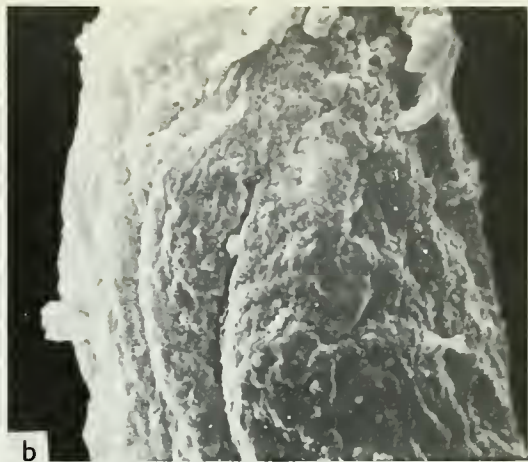
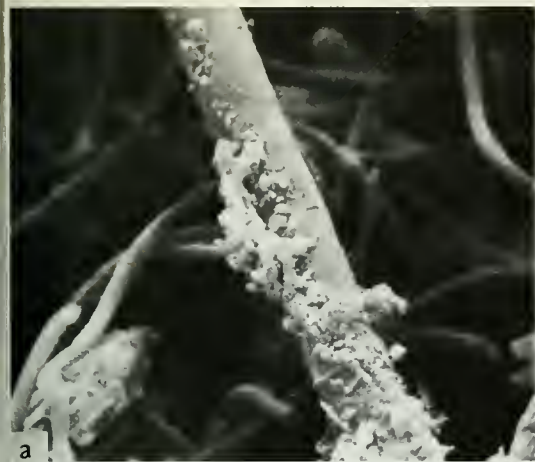
Point 1 in the list of *Girvanella*'s generic characteristics (p. 88), is of descriptive value only. Most cyanophytes are microscopic<sup>1</sup>. Unless the calcification is incomplete, the structure is bound to be tubular (2), and no noncalcareous, mineralized forms have yet been reported (3). Some modern cyanophytes can approximate rectilinear growth (4), but it is not a consistent feature at generic level. It is also difficult to say when a curve is slight enough to be treated as incidental, except perhaps in a population study.

Some modern genera are habitually spiral (*Spirulina* Turpin); others are spiralled at times (*Oscillatoria* Vaucher) and many are never more than sinuous (*Rivularia* Agardh.). The characteristic seems to be both environmentally and genetically controlled. Comparison with *Oscillatoria* suggests that occasional spiralled filaments may be acceptable, but that populations with habitually spiralled filaments such as *G. problematica* var. *spiralis* Lewis should be excluded from the genus. Since procaryote cells seem to be either circular or oval in cross section (5), their trichomes are bound to have this shape. However, the carbonate tubes which form around them are not trichomes, and their inner surfaces may have several controls. If the carbonate is an impregnation, or a combined impregnation and encrustation, its inner surface may conform to the surface of the trichome. It will then be circular in section. No such restriction applies to the inner surface of an encrustation, which will more or less follow the surface of the sheath. Many cyanophytes have smooth sheaths with circular cross sections. However, the sheath may be irregular, or it may have a sculpture such as spiral or annular ribbing. This is probably an environmentally-determined character, in part if not entirely. It may also reflect the fine structure of the sheath itself. *Scytonema* Agardh., for example, has a strongly fibrillar sheath (Singh 1954). Unless the nature of the calcification is known, therefore, it would seem best to describe the calcareous tube of *Girvanella* as approximately circular in section, and perhaps to give an acceptable range of variation.

It has been suggested that the calcareous tube of *Girvanella* is an impregnated sheath (Seward 1898) but there is evidence for the presence of both impregnations and encrustations in the Stinchar Limestone girvanellids (Danielli 1977). It is possible that these should

<sup>1</sup>Some bacterial carbonates are visible to the naked eye and resemble porostromates, but their importance in the fossil record is not yet known.

**Fig. 4** Types of calcification in Recent blue-green algae. Several genera are shown, and grain size varies considerably, but the grain shapes are on the whole similar. (a), encrustation of equidimensional grains on a relatively smooth filament. Note the uncalcified background filaments. Bar = 15  $\mu$ m. (b), impregnation, indicated by the granular appearance of the sheath surface. Bar = 2  $\mu$ m. (c), embedding in a mass of mucus strands. c calcite grains, m mucus strands. Bar = 2  $\mu$ m. (d), an empty but impregnated sheath which might be preserved as a porostromate fossil. Bar = 2  $\mu$ m. (e), encrustation and impregnation of the same sheath, the two carbonates having similar textures. Bar = 1  $\mu$ m. (f), a rivulariacean calcite. The trichome and sheath lay in the hollow, becoming encrusted with equigranular calcite. Organic matter has been removed with 14% NaClO in this case, exposing the micritic texture of the calcite. In the light microscope these tubes often appear uncrystalline owing to optical continuity of the grains. Bar = 50  $\mu$ m.



be separated into two genera, although clear support for such a split cannot at present be obtained from modern organisms. *Rivularia*, for example, can both encrust and impregnate at the same time, and the two often have inseparable textures. In addition, the criterion of the internal to external diameter ratio, used for example by Riding (1977) to distinguish between them, does not hold in many cases. The impregnated sheath may be very thick in proportion to the protoplast diameter, and encrustations may be thin. These variations seem due mainly to ecological factors.

The cylindrical nature of the tubes (7) implies that the diameters are fairly constant along the tube axis, and that the structure is not branched. Some modern cyanophyte trichomes have a constant diameter (e.g. *Phormidium* Kuetz.), some taper (*Rivularia*), and some have pronounced constrictions at cross walls (*Nostoc* Vaucher). Whether or not this would be reflected in the carbonate again depends on the nature of the structure. A constricted tube would probably indicate that the filament it contained was also constricted, and would also be quite good evidence that the filament was simple, but a carbonate tube without constrictions gives no evidence either way.

Tapering would probably be reflected by the internal diameter of the tube, although not necessarily by the external diameter, if the tube were an impregnation. Since part of the carbonate of *Girvanella* tubes may well have been an impregnation, tapering might be expected to be apparent. It is then possible to say that the trichomes of *Girvanella* were probably not tapered.

The presence or absence of branching is used at generic level in the identification of modern cyanophytes (West & Fritsch 1927 : 454). It is not possible to separate false from true branching unless the trichomes are present, of course. Some porostromates, such as *Ortonella* Garwood 1914, have clear branching, but *Girvanella* is by implication an unbranched form (Dricot & Tsien 1977 : 232). Branching need not be frequent, so careful searches are necessary to establish its absence from any population.

Some modern cyanophytes have thin strips of sheath lying between the cells of their trichomes (*Nostoc piscinale* Kuetz.). Other forms often have fragmented trichomes, with sheath separating the fragments at more or less regular intervals (*Scytonema fuliginosum* Tilden). It is theoretically possible for the strips of sheath to become impregnated with carbonate, producing a septate tube which could be preserved (9). However, no example of a septate *Girvanella* has been described which will support careful study.

Having scrutinized the original diagnosis of *Girvanella* above, it is clear that an emendation would be of some value. An attempt is offered below, taking these points into consideration.

### Systematics

Kingdom PROCARYOTAE Buchanan *et al.*, 1974

Division CYANOPHYTA Smith, 1938

Class uncertain

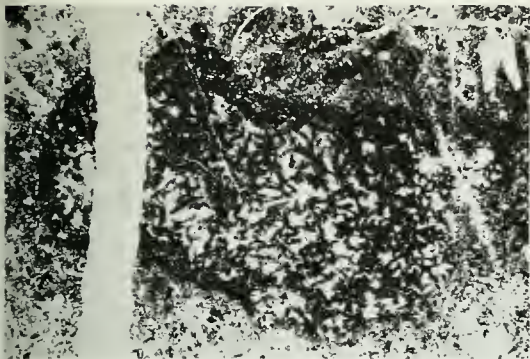
Family POROSTROMATA Pia, 1927

Genus *GIRVANELLA* Nicholson & Etheridge, 1878

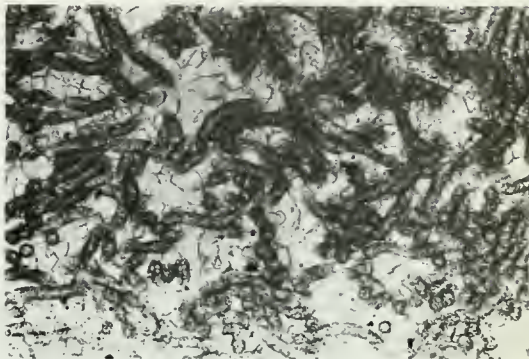
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Fig. 5 The neotype of *Girvanella*, and some contrasting growths in the same thin section, BM(NH) V 34566. (a), the growth which Wood (1957) designated as neotype of *G. problematica*. Note the low density central region, with denser growth at the boundaries. Bar = 55  $\mu$ m. (b), a detail of (a), corresponding to Wood's (1957) figure, showing low density, moderate sinuosity, local parallelism and adherence. Bar = 100  $\mu$ m. (c), detail of (b), with a variety of cell space textures. Bar = 50  $\mu$ m. (d), part of the same growth showing variable sinuosity, density and parallelism. Bar = 100  $\mu$ m. (e), another growth in the same section, with parallel, adherent tubes; note the cement overgrowth (c). Bar = 100  $\mu$ m. (f), a third growth in the same slide, with thin sinuous tubes arranged more or less randomly. Bar = 200  $\mu$ m.

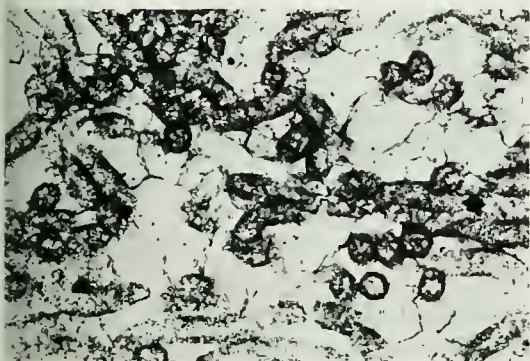




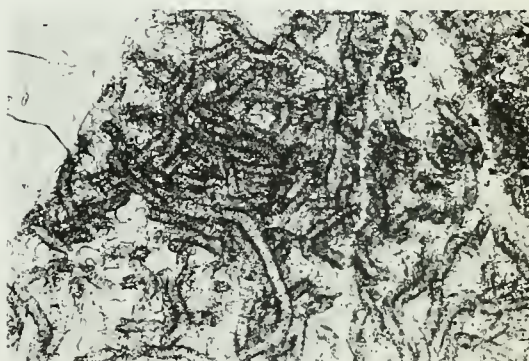
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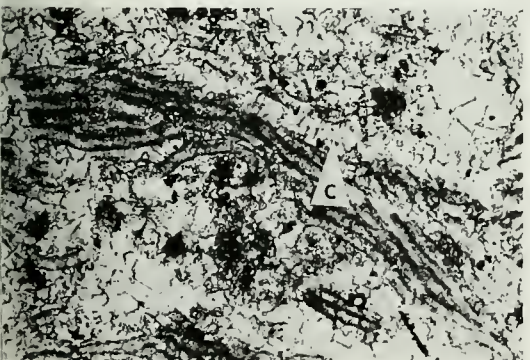
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[= *Argirvanellum* Rothpletz, 1916; *Batinevia* Korde, 1966; *Botominella* Reitlinger, 1959; *Fistulella* Korde, 1973; *Kenella* Korde, 1973; *Nicholsonia* Korde, 1973; *Siphonema* Bornemann, 1886; *Sirephochetus* Seely, 1885; *Stromatocerium* Miller, 1882].

RANGE. Upper Proterozoic to Middle Cretaceous.

DIAGNOSIS. Microscopic tubular encrustations and/or impregnations of sheaths of filamentous organisms; filaments arranged at random or prostrate, rarely vertically; filaments single or in growths of variable size, shape and density; orientation parallel to random; filaments unbranched and slightly to highly sinuous; cell space approximately circular in cross section, sometimes compressed or with slight irregularities; cell space usually occupied by cement spar but sometimes micritic, cement developing either by growth from grains in the micritic tube or independently, as druses or equidimensional particles; aseptate micritic calcite tube comprising prisms or equidimensional grains, or both, the prisms with their long axes arranged perpendicularly to the filament axis and in a single layer, sometimes with smaller intercalated prisms.

NEOTYPE. The specimen shown on Fig. 5, after Wood (1957). Thin section kept by the Palaeontology Dept. of the British Museum (Natural History), London, reg. no. V 34566.

HORIZON AND LOCALITY. Stinchar Limestone (Ordovician, Lower Caradocian Series), Tormitchell Quarry near Girvan, Ayrshire, Scotland.

### Specific subdivision

As Wood (1957) found, specific subdivision of *Girvanella* is a difficult problem. He drew a graph of internal diameters and obtained a bimodal curve for the sample he took from the

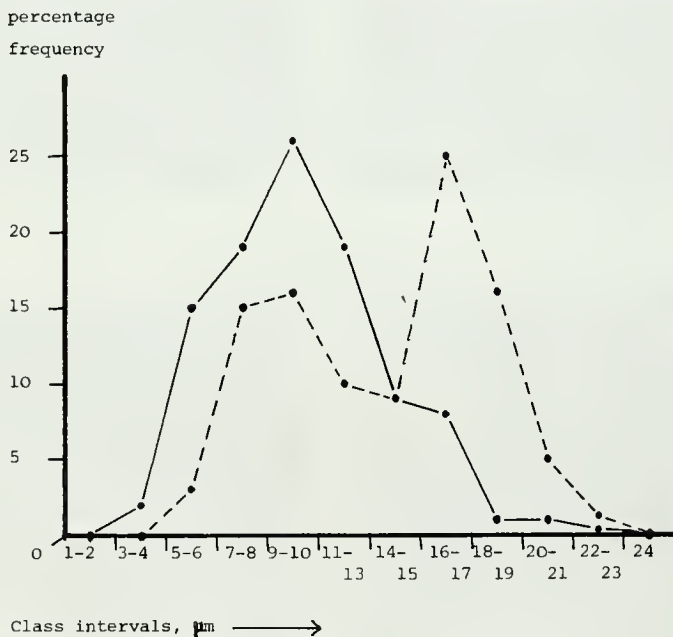


Fig. 6 Internal diameters of *Girvanella* tubes from the Stinchar Limestone. Plain line, Aldons Quarry (Danielli herein,  $n=1060$ ). Pecked line, Benan Burn and Tormitchell Quarry (after Wood 1957, with permission;  $n=633$ ).

Stinchar Limestone. The external diameters gave a less useful curve. Internal diameters from the sample collected for the present study gave a unimodal plot with a slightly longer range (Fig. 6). Wood's material came from several localities, and thus could have been derived from environments which differed in biological or biochemical factors but which are indistinguishable by modern geological methods. If this is so, the algae are likely to have been different in each. Even if the same species were present in all, several ecophenes may have been represented. The Aldons Quarry sample came from a single outcrop and is not therefore strictly comparable with Wood's.

Mamet & Roux (1975: 137) surveyed the Carboniferous and Devonian species of *Girvanella*, and condensed the various taxa into four species. Their method of measuring from the published figures rather than the type material is questionable, but the results are of some interest. They based the four species on a graph of tube thickness plotted against internal diameter. Unfortunately, girvanellids in the Stinchar Limestone at Aldons Quarry do not conform to Mamet & Roux's method of subdivision. Nor does the method allow for the presence of a fifth species. The internal diameter and tube thickness of the Aldons sample are similar to those of Mamet & Roux, but the measurements are distributed over most of the graph and do not fall into clusters.

In a case like this reappraisal of the genus as a whole is necessary. One approach might be to reanalyse the previously-designated types, and reorganize them. However, as pointed out by Raup & Stanley (1971: 177), many types do not adequately represent their species. Skevington (1973: 43) has come to a similar conclusion in the case of graptolites, and Hughes, Drewry & Laing (1979: 515) have regretted the type and synonymy arrangement of taxa under the rules of botanical nomenclature for a similar reason. Since a complete reassessment of the species of *Girvanella* would require a work of far greater length than this, and fundamental studies in greater depth, no more is intended here than to suggest a possible approach using the definition of the type species *problematica*. The species is taken as described by Nicholson & Etheridge (1878). The existing classification of *Girvanella* species has been investigated, but the value of *species inquirendae* in a systematic re-evaluation is open to question. It will be shown that some new basis for subdivision of the genus is needed, if the classification is to reflect the biology of the organisms.

The characteristics used by Nicholson & Etheridge (1878) give a good description of the fossil, and may be summarized as follows: (1) sheath diameter; (2) tapering; (3) parallelism; (4) density; (5) sinuosity; (6) growth shape; (7) growth size. No tapering species have been described (2). Indeed, since the generic diagnosis implies that the tube diameter is constant, the question might be considered out of place here. The density of the growths (4) has also been discussed under generic characteristics.

Points 3, 5, and 6 are concerned with the spatial relations between tubes. Authors delineating species have often described the sinuosity of tubes, and sometimes their degree of parallelism. Unfortunately no attempt has been made to define these numerically. Much the same can be said of growth shape and size. There is, however, some justification for this if one agrees with Maslov's (1949) view that they are environmentally-determined characteristics. This is likely to be the case, in view of the phenotypic plasticity of Recent filamentous cyanophytes (Desikachary 1970, Rippka *et al.* 1979).

We are left with point 1, sheath diameter. It has been used by many workers, in both definition and identification of species. The diameters of many of the species listed in Table 2, pp. 82-4, are compared in Fig. 7. The first problem encountered is the meaning of 'diameter'. As shown in Fig. 1 (p. 80) there are two diameters *cd*, *ef* to any cross section. In *Girvanella* they may differ by a factor of two or more. Not all authors of *Girvanella* species have explained which diameter they were giving.

The diameters shown have considerable overlap, and the ranges differ in length. Measurement of a single tube will not allow assignment of the tube to one species. If a number of tube diameters are known for a sample, questions of sample size and statistical significance are raised. Wood (1957) measured about 600 tubes, and found the range 5  $\mu\text{m}$  to 22  $\mu\text{m}$  for the Stinchar Limestone. Over 1000 were used in the present study, and a slightly wider range was

obtained (Fig. 6). This might have been extended even further if 1500 tubes had been measured. Green (unpublished, 1959) conducted a statistical study of some Silurian *girvanellids*, but the conclusions were published without the basic data (H. M. Johnson 1966).

The external diameter is a function of the internal diameter and tube thickness. Its significance has been discussed by Wood (1957 : 26), who considered it to be unreliable because of its dependence on environmental factors. However, Mamet & Roux (1975) have shown that the relationship between tube thickness and internal diameter may be useful in classification.

*Girvanellids* in the sample taken from the Stinchar Limestone at Aldons Quarry agree with the generic definition of Nicholson & Etheridge (1878) in most respects. However, growth densities vary from 10% to almost 100% (Fig. 3). Strictly, the high density growths are not *Girvanella*, but in every other way the growths fit the definition. Since growth density is probably an environmentally-determined characteristic, there seems to be no reason for separating these forms as a different genus or species from the lower density forms.

The internal diameter from the Aldons Quarry sample ranges between 4  $\mu\text{m}$  and 22  $\mu\text{m}$  (the area indicated in Fig. 7). Some 26 species are contained in this interval, and it is overlapped by 10 others. It is possible that, if the sample size were larger, some of these species would lie completely within the Aldons range.

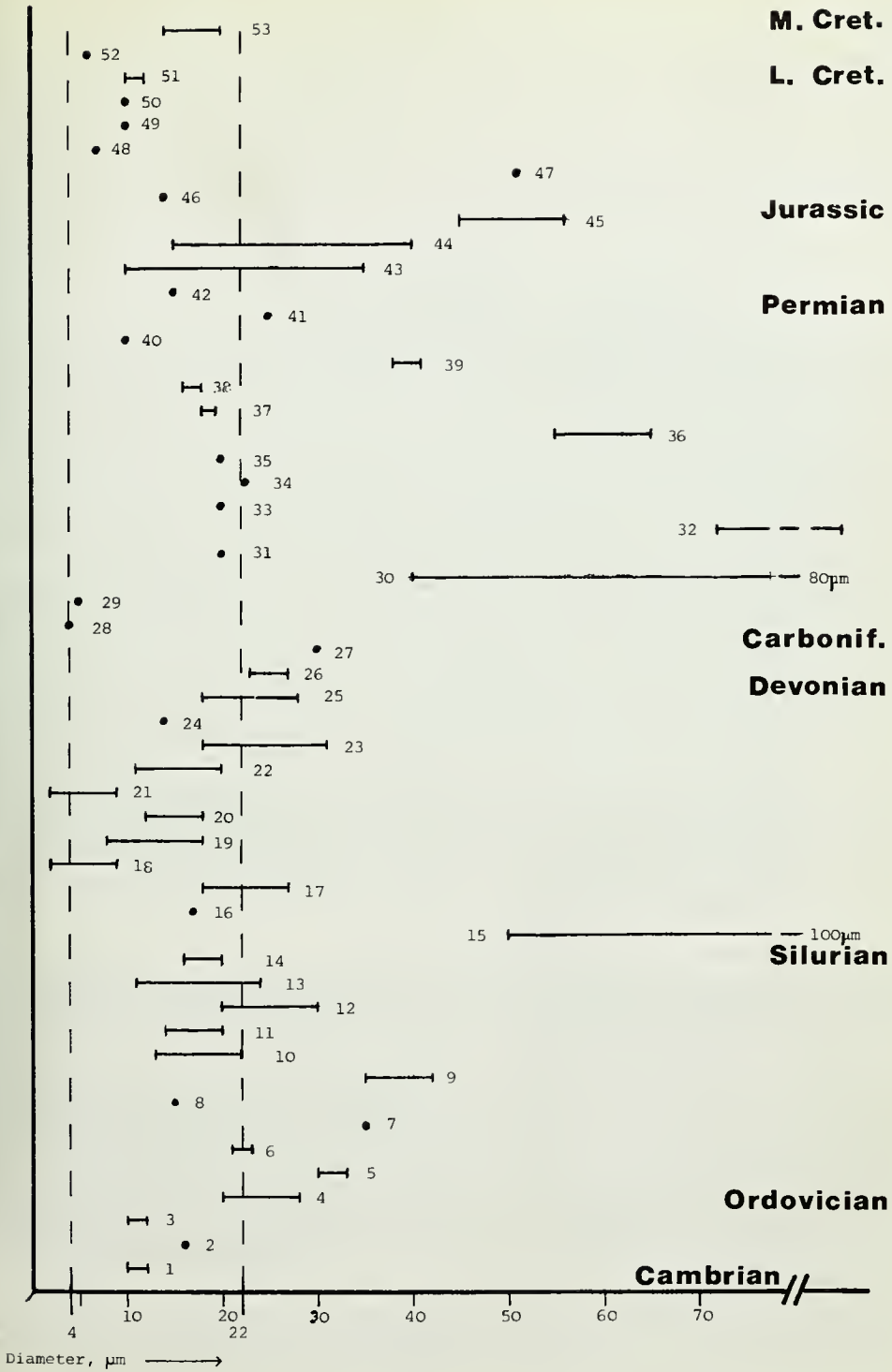
The external diameter of each tube was measured, and tube thickness was determined as half the difference between the two diameters. A range of 0.5  $\mu\text{m}$  to 22  $\mu\text{m}$  was found, which includes all those species whose definitions include a value for tube thickness. To illustrate the variability of the growths as well as that of individual tubes, Fig. 8 gives the internal diameter and tube thickness ranges found in some particular growths. While examples of the extreme values are rare, objections of a statistical nature can be made to the exclusion of specimens on grounds of rarity.

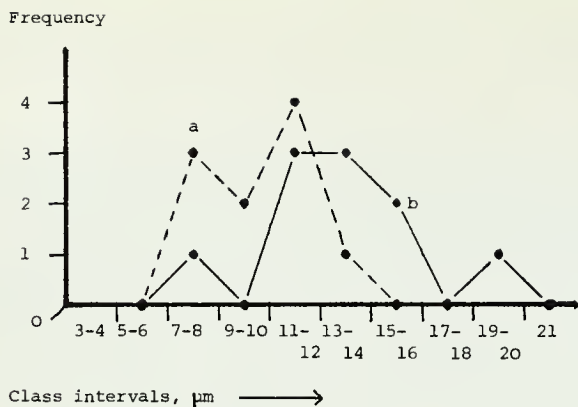
A study of *Girvanella* populations throughout its fossil record is evidently the next stage in this reassessment. The example of Rippka *et al.* (1979), in leaving this to the future, is followed here, but some aspects of the organism which might be considered are the detailed microscopic morphology in relation to the ecology of the organism, the nature of the carbonate tube and its relation with the enclosed trichomes, and the ultrastructure of the carbonate tube in relation to other Porostromates and to modern calcified cyanophytes.

The work of Drouet is applicable to the first of these suggestions. Though now his classifications are generally rejected, he did demonstrate the dependence of cyanophyte morphology on environmental factors, describing ecological variants or ecophenes of, for example, *Schizothrix calcicola* (Ag.) Gom. (Drouet 1963). These varieties have essentially the same genotype. *Girvanella* comes from a wide geographical and temporal range, as well as a wide range of ecologies. There must be many genotypes represented, so that the ecophene approach will only be tenable in some circumstances. It might be used with advantage within a single outcrop, and preferably at a single horizon, for determining local variability within a population.

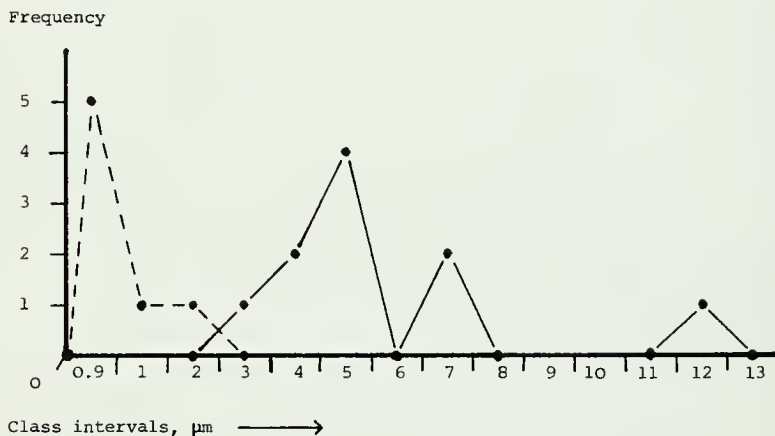
Huxley (1938) defines a cline as any variational trend in space. If the end members of a cline are separated from each other, they may develop into distinct species. In the case of fossil material especially, the full cline may not be preserved and the end-members may be taken for different taxa. Thus genotypic variation occurs along the cline. This picture, suggested by Dr M. A. Edington (personal communication), fits *Girvanella* a little better than does that of ecophenes.

Fig. 7 The diameters of *Girvanella* species. Ranges are given in chronological order, and keyed to Table 2, p. 82-4. Most authors give internal diameters, but some do not specify which they provide. Since the sparry cell space is often easy to see, it is likely that most of these undefined diameters are in fact internal. The range of values from the Aldons Quarry sample is indicated by two vertical broken lines. The variability of the lengths, overlapping positions, and lack of frequency distributions of the individual species makes the diameter of low value as a taxonomic criterion at present.





a) Internal diameter; a. N=10, b. N=10.



b) Tube thickness; a. N=7, b. N=10.

Fig. 8 Internal diameters (a) and tube thicknesses (b) for *Girvanella* growths in the Stinchar Limestone at Aldons Quarry. Plain lines, maximum range for single growth. Pecked lines, minimum range for single growth.

The study of clines requires sampling over substantial areas, since clinal variation is a geographical phenomenon. Therefore an investigation of *Girvanella* clines would require collection along the same horizon, over some kilometres if possible. Since no study of this kind has yet been published, it is not possible at present to decide whether *Girvanella* does or does not form clines.

The second suggestion for future studies concerns the carbonate tube. Its relationship to the original sheath of the organisms greatly affects the acceptable range of variation of characters such as the internal diameter. Unless such questions can be answered, these ranges must remain arbitrary.

Turning to the third suggestion, there is in fact some reason to doubt the value of ultra-structure as a taxonomic tool in the case of cyanophyte carbonates. Recent organisms show no clear relationship between carbonate fine structure and species or even genus. In addition

the fossil porostromate *Rothpletzella gotlandicum* Wood 1948 appears to have a similar ultrastructure to that of *Girvanella* (Fig. 2, p. 89). Kobluk & Risk (1977: 1077) have reported girvanellids with similar textures to those of the Stinchar Limestone forms. This apparent stability of the carbonate texture from place to place is interesting, but not very promising for specific subdivision.

The importance of population studies in work of this kind cannot be over-emphasized, especially with organisms that show such degrees of variation. In these cases a range of variation should be given for every characteristic.

### Conclusions

The morphology of *Girvanella* has been subject to a good deal of misinterpretation. The genus has been discussed here in terms of modern cyanophytes, and the limitations of the fossil material have been outlined. Direct comparison can only be made at the level of filaments, since there is at present no unequivocal evidence concerning trichome shape, or number per filament.

The generic diagnosis of Nicholson & Etheridge (1878) has been emended to take account of this discussion, and the specific subdivision of the genus has been considered briefly. Studies involving sampling over wide areas, at a single horizon, are considered necessary so that the variation shown by the fossil can be investigated.

The position of the genus in relation to the groups of modern filamentous organisms is at present indeterminable, the only guide being the lack of branching shown by *Girvanella*. Russian scientists such as Kulik (1973: 39) have defined species as members of the Hormogoneae and the assignment is very possibly correct, but care should be used in such determinations. The remarks made by Edhorn (1979) concerning the mobility of the filaments appear to present an over-extension of the evidence available from the fossil material and would be difficult to test. However, comparisons like that of Edhorn, between the growth habits of *Girvanella* and those of Recent organisms, may shed some light on the ecology of the fossil if applied with caution.

It is at present possible to say very little about the organisms concerned in the formation of *Girvanella* tubes. Population studies coupled with ecological work on the communities associated, and with sedimentology, may be useful in this connection. Since cyanophytes are important members of many modern communities, and are major sediment-producers at the present time, fossil forms might be expected to be of considerable palaeoecological value.

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